Growth of the shoot apex of *Lupinus albus* observed by surface photomicrography and histology

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Summary: Surface views of the shoot apex of *Lupinus albus* at various developmental stages, referred to as plastochron stages, were photographed by reflected light. A part of the apical surface was shown in a flat montage of surface photomicrographs. A part of the area photographed was then cut paradermally, and cell configurations in surface views were compared with those in sections. The cells derived from individual cells in the surface of the shoot apex of an embryo, referred to as "initial cells", remained for a time within the original walls, which were stretched and became thickened. Thus, the surface layer of the shoot apex of a young plant consisted of many packets of cells, "primary cell groups", encompassed by the thickened original walls, as revealed by surface photomicrographs and paradermal sections. As the plastochron stages proceeded, these cell groups became enlarged in area due to an increased number of derivatives by cell divisions, until the encompassing walls became stretched and obscure, due to increase in cell number. These cell groups proved to be useful for the study of growth in the shoot apex, and the analytical consideration of surface growth of the shoot apex was made.

Key words: initial cells, *Lupinus albus*, shoot apex, surface growth.

Introduction

Several published observations on the histology of the shoot apex of vascular plants have depicted packets of cells surrounded by a thickened wall (Ball, 1949; Gifford, 1950; Boke, 1951; Mia, 1960). These studies gave graphic demonstrations of cell groups within the shoot apex, mostly in the inner tunica layer and the corpus, based mainly upon longitudinal and transverse sections of the meristem. Bierhorst (1977) illustrated cell groups in surface photomicrographs of a wide variety of filicalean ferns, and utilized their occurrence to substantiate his interpretation that the growth of these shoot apices is derived from divisions of the apical cell.

The tentative interpretation often given by the above authors is that the packet of cells is derived from the divisions of an original initial cell and its derivatives, all within the stretched and thickened original wall. If this interpretation is valid, then it would be expected that the number of cells included within a packet may increase as time passes, and further, if there is variation in cell number in different packets, this difference may be explained as a result of different rates of cell division during the same period of time.

The present paper describes the results of observations of the surface of intact shoot apices of *Lupinus albus* and of histological confirmation by paradermal sections.
Special emphasis is given to the formation of the packets of cells and to the increase in number of their constituent cells at various locations on the apical surface during seed germination and subsequent growth.

**Materials and methods**

Seeds were imbibed with water for 24 hours, and were sown in a plastic box filled with a mixture of wet sand and peat moss. They were kept in a growth chamber at a constant temperature of 25°C, illuminated at 7000 lux for 12 hours light per day. A balanced mineral solution was applied to the box once per week.

The terminal 2 cm of a plant were excised after soaking. The cotyledons and all unfolded leaves were removed, and folded young leaves and foliar primordia were also excised by a micro-scalpel under a dissecting microscope, leaving the youngest three foliar primordia, which were named P₁, P₂, and P₃ respectively in sequence of development, P₁ being the youngest (Fig. 1A). The future positions of foliar primordia to arise were labeled in sequence as I₁ and I₂. The shoot tip with its foliar primordia and subjacent tissues was then cut to ca. 3 mm in length and fixed on a small stage of the shoot apex holder, a kind of goniometer, which is a special device for holding a small piece of tissue at a desired angle (Soma, 1978). The holder was clamped onto the mechanical stage of a microscope (Vanox, Olympus Optical Co) equipped with an axial illuminator (Neopak, Olympus), which has an optical system similar to that of a metal microscope. Surface photomicrographs of the shoot apex were taken by reflected light with an automatic photomicrographic apparatus (PM-10A, Olympus) to include vertical and lateral views. Sometimes it was necessary to excise the upper portion of P₂ and P₃, because it prevented photography of the apical flank near their axils.

Immediately after surface photomicrographs were taken, the shoot apex was fixed in CRAF III (Sass, 1958), dehydrated and infiltrated by the t-butanol method, and embedded in Tissuemat. In order to orient precisely the shoot apex for later sectioning, one side of the shoot tip parallel with the proper plane was cut off under a dissecting microscope prior to fixing. This cut surface permitted precise orientation of the shoot tip during subsequent sectioning. Sections were cut serially at 8 μm, and stained with Heidenhain's hematoxylin and fast green.

**Scanning the apical surface.** It should be noted that the upper portion of the apical dome of this species could be regarded as a portion of a sphere, because the lateral outlines of the apical dome in two photographs taken at right angles to each other coincided respectively with an arc of the semi-circles having the same radius (Fig. 1B, C). Because of its spherical curvature, only a small area of the apical surface was observable in a single visual field at a high magnification. Therefore it was necessary to locate successively each area into the visual field by tilting the shoot apex around the horizontal axis as well as by turning it around the vertical axis in order to scan the curved apical surface. The minimal angular interval between two adjacent areas observed was 15 degrees.

The longitudinal position of each observed area was represented in degrees of the meridian (M). The line connecting the apical summit and the center of P₁ was defined as 0° M (Fig. 1A). The apical summit was determined in the vertical view fairly precisely in regard to the centers of three youngest foliar primordia, which were
Figure 1. Photomicrographs of the shoot apex, P₁ being the 29th leaf after the cotyledons. A, Vertical view. B, Lateral view taken from the direction along 90° M, P₃ having been removed. C, Lateral view taken from the direction perpendicular to that in B. Asterisk and white arrow-head indicate the apical summit (The same explanation in the subsequent figures). Arrow in A indicates the direction of the genetic spiral. o, center of the semi-circle of which arc coincides with the outline of the upper portion of the apical dome. r, radius of the semi-circle. All, ×147.

disposed successively at a divergence angle of approximately 137°. Degrees (M) from 0° to 180° are plus toward the progressive direction of the genetic spiral, as shown by an arrow, and minus toward its regressive direction (Fig. 1A).

Since an outline of the surface seen from just above the apical summit at high magnification was approximately circular because of its spherical curvature, the apical summit was determined as its center, which corresponded to 90° L (latitude) (Fig 1B). The surface viewed by tilting the shoot apex by 15 degrees along any meridian was also circular of which center corresponded to the point at 75° L. In the present study, the distal portion of the apical dome above the level of 75° L was called the “summit area”, which was represented as a circle around the apical summit in the vertical and surface views of the shoot apex (Figs. 1A, 5A and 6A), and the portion of the apical dome between 75° L and the axils of P₁, P₂ and P₃ was called the flank. The summit area has no particular meaning as the “central zone” used generally in the developmental studies of the shoot apex, but it was employed here only for describing the area around the apical summit.

The surface viewed by tilting the shoot apex by more than 30 degrees was not always circular, sometimes elliptical or irregular in outline according to the complicated surface curvature, especially in the lower portion of the flank. Therefore, the flank along a given meridian was divided into three parts of equal length, termed upper, middle and lower flanks respectively (Fig. 6A). Thus, any position on the flanks could be indicated both by the degrees of meridian and by one of three flank parts.

Montage of surface photomicrographs. The marginal portion of each photographed area of the apical surface was included in the adjacent photographs
taken by tilting at 15 degrees because of the depth of focus of the objective. Thus, a series of photographs taken along the same meridian could be put together to make a montage, which showed a part of the curved apical surface as a flat band. Furthermore, any montage of photographs along a certain meridian could be put together laterally with another one along the adjacent meridian. The radius of the summit area in such a montage photograph was determined by the distance between the centers of the two connected individual surface photomicrographs taken respectively at 90° L and 75° L.

**Observations**

Under the present culture conditions the shoot apices remained in the vegetative phase of growth and continued to form only foliage leaves throughout the period of cultivation. For the present study, 178 shoot apices were examined. The youngest plants were taken two days after soaking. The oldest plant was observed 63 days after soaking, and it had 40 leaves and leaf primordia.

The total number of leaves and foliar primordia in each plant was plotted against the period of days after soaking (Fig. 2). The relation between them was linear. The formula indicated in the figure means that the plants produced leaves at a fairly constant interval. The average plastochron based on linear regression was about 1.8 days: this is much shorter than 3.0 or 3.2 days reported for the same material in our previous paper (Soma and Ball, 1963). This difference may be due to culture conditions.

![Figure 2. Rate of leaf initiation. R, Correlation coefficient. PL, Plastochron.](image)

**Shoot apices at 6th through 8th plastochron stages.** The term, "plastochron stage" is used here to indicate the developmental stage of the shoot apex. When P₁ is the 6th leaf after the cotyledons, the shoot apex is at the 6th plastochron stage, and so on. Usually six to eight, mostly seven foliar primordia were already present in the mature seed. These foliar primordia might have been formed during late embryogeny. Fig. 3A shows the apical surface around the summit of the shoot apex at the 6th
plastochron stage two day after soaking. Each superficial cell was turgid and convex in form, and was surrounded by thin anticlinal wall. A paradermal section of the same area showed that none of these cells had yet divided, because neither mitotic figure nor partition wall was found in them (Fig. 3B).

The shoot apex at the 8th plastochron stage observed 3 days after soaking is shown in Fig. 4A, B. Most of the superficial cells, #1~#6, around the apical summit were all obviously undivided in surface as well as sectional views. In the outer walls of both cells, #7 and #8, however, there were shallow furrows across them. The paradermal section confirmed that there was a partition wall beneath each furrow. Thus, these furrows were considered to have appeared as a result of recent cell divisions.

Figures 3 and 4. 3, Shoot apex at the 6th plastochron stage two days after soaking. A, Montage of the surface photomicrographs showing an area around the apical summit. B, Paradermal section cut through the same portion as in A. The same numbers in A and B show the same cells (The same explanation in the following figures). ×640. 4, Shoot apex at the 8th plastochron stage three days after soaking. A, Single surface photomicrograph showing an area around the apical summit. B, Paradermal section cut through the same portion as in A. ×640.

Fig. 5 also shows the shoot apex at the 8th plastochron stage four days after soaking. Within the summit area most of the cells seemed to be single in surface view (Fig. 5A, B). However, the paradermal sections revealed that the cells labeled with #1~#11 had already divided, and the cell #12 was in metaphase of mitosis (Fig. 5C, D). The other ten cells within the summit area were obviously still unpartitioned. The original wall surrounding each pair of daughter cells was clearly thickened and more darkly stained than the new partition wall (cells #4, #9, #10 and #11 in Fig. 5C, D). The reason why
the partition walls between daughter cells could not be reproduced in the surface photomicrograph may be because these walls were still too thin to reflect the light beam.

Figure 5. Shoot apex at the 8th plastochron stage four days after soaking. A, Montage photograph showing the summit area. B, Surface photomicrograph showing a part of the summit area taken at higher magnification. C, Paradermal section cut through the summit area. D, Paradermal section cut at 8 μm lower than that in C. A, ×520; B, C, D, ×640.

Shoot apex at 10th plastochron stage. The shoot apex at the 10th plastochron stage observed 7 days after soaking is shown in Fig. 6. The lateral view of the apical dome showed that the upper flank along 135° M had slightly bulged out, indicating that the apex was just prior to the formation of the next foliar primordium (Fig. 6E, right part of the dome). The montage photomicrographs showed that the superficial cells within the summit area were seemingly single, while the flank consisted of many groups of cells (Fig. 6A). By referring to the paradermal sections cut through the flank, it was revealed that the cell #1 at the margin of the summit area was actually a group of two cells (Fig. 6B). It is likely that other cells within the summit area might actually be cell groups, each consisting of small number of cells, though the section had not been cut through the summit area here. The cellular configurations in these selected groups of cells are illustrated diagrammatically in Fig. 6D. By referring to the patterns of partitioning walls between constituent cells in surface as well as sectional views, the sequence of wall formation after the first one was easily discernible for some cell groups. It should be noted that a group located in the middle flank consists of more cells than that located in the upper flank.
Figure 6. Shoot apex at the 10th plastochron stage seven days after soaking. A, Montage photograph showing the apical surface along 0° M, 120° M and 135° M. Oblique white bar in upper left indicates the axil of P1. Two broken arcs indicate the boundary between upper and middle, middle and lower flanks respectively. d, debris (the same abbreviation in the following figures). B, Paradermal section cut through the upper flank. C, Paradermal section cut through the middle flank. D, Diagrammatic illustration of cell groups #1-#7; out of all the constituent cells in each group, only those derived from one of the daughter cells produced by the first division of the initial cell are numbered. Thinner partition walls in each cell group indicate more recently formed ones. Cross marks indicate the injured cells. E, Lateral view of the shoot apex taken from the direction at right angles to the median line through 135° M and −45° M. Broken arc depicts the outline of the apical dome defined as a semi-circle. Oblique white line indicates the orientation of the sections in B and C. A, ×400; B,C, ×600; E, ×120

Table 1 shows that the surface area of each cell group increases with the increasing number of constituent cells and also with increasing latitudinal distance from the summit area, although the difference in area between cell groups in the middle flank and those in the lower flank is small. It is also noticeable that the average cell area in each group decreases with increasing number of constituent cells.
Table 1. Latitudinal position, number of constituent cells, area and average area of constituent cells of cell groups #1-#10 shown in Fig. 6.

<table>
<thead>
<tr>
<th>Cell group</th>
<th>Latitudinal position</th>
<th>No. of constituent cells</th>
<th>Area* (µm²)</th>
<th>Average area of constituent cell (µm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>#1</td>
<td>75° L</td>
<td>2</td>
<td>317</td>
<td>158.5</td>
</tr>
<tr>
<td>#2</td>
<td>upper</td>
<td>3</td>
<td>389</td>
<td>129.7</td>
</tr>
<tr>
<td>#3</td>
<td>flank</td>
<td>6</td>
<td>238</td>
<td>79.3</td>
</tr>
<tr>
<td>#4</td>
<td>flank</td>
<td>9</td>
<td>469</td>
<td>78.2</td>
</tr>
<tr>
<td>#5</td>
<td>middle</td>
<td>15</td>
<td>552</td>
<td>61.3</td>
</tr>
<tr>
<td>#6</td>
<td>flank</td>
<td>18**</td>
<td>1006</td>
<td>67.1</td>
</tr>
<tr>
<td>#7</td>
<td></td>
<td></td>
<td>1155</td>
<td>64.2</td>
</tr>
<tr>
<td>#8***</td>
<td>lower</td>
<td>739</td>
<td></td>
<td></td>
</tr>
<tr>
<td>#9***</td>
<td>flank</td>
<td>1153</td>
<td></td>
<td></td>
</tr>
<tr>
<td>#10***</td>
<td>flank</td>
<td>1213</td>
<td></td>
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</tr>
</tbody>
</table>

*Measured with a planimeter for the surface photomicrograph shown in Fig. 6A.

**Since cell group #7 was obviously injured at its lowest right portion (Fig. 6C), actual number of constituent cells could be one or two more.

***Actual number of constituent cells was not known, since the paradermal section had not been cut through these cell groups.

Shoot apex at 11th plastochron stage. The shoot apex taken seven days after soaking is shown in Fig. 7. Here, the packets of cells had also become obvious in the summit area (Fig. 7A). More constituent cells could be counted in some of these packets of cells (Fig. 7C) than in the shoot apex at the 10th plastochron stage (Fig. 6). Therefore, it may be noted that the cells in the summit area continue to divide as the plastochrons proceed. It was evident that the cell groups in the flank along 180° M (right in Fig. 7A) were larger than those in the summit area. When the surface of P₁ was focused, a large cell group was also found there (Fig. 7B). The cells on the flank as well as those on P₁ divided more frequently and thus produced more derivatives, forming larger cell groups than those in the summit area.

Shoot apex at 17th plastochron stage. Fig. 8A shows a montage of surface photomicrographs on the plus side of the meridians in the shoot apex taken 17 days after soaking. Although the summit area still consisted of a few packets of cells, packets were hardly discernible in the flank, especially in the apical sector between 90° M and 180° M. Careful observations revealed that a portion of the thickened wall surrounding a packet of cells had faded out in several places in the flank (arrows in Fig. 8A). It is probable that such thickened walls had been stretched by proliferation of constituent cells and had become too thin to be recognized by surface photomicrography. In addition, it should be noted that the superficial layer of cells on the flank around 135° M, where the next foliar primordium was to arise, consisted of many radial rows of cells as described for the shoot apex of Clethra barbinervis by Hara (1971).
Figure 7. Shoot apex at the 11th plastochron stage seven days after soaking. A, Montage photograph showing the apical surface along the median line through 0° M and 180° M. Vertical line on the left indicates an approximate position of the inflection point between the apical dome and P₁, which is also indicated in B and D by an arrow. B, Surface photomicrograph of P₁, showing the cell group on its adaxial surface. C, Paradermal section through the summit area. D, Lateral view of the shoot apex. A, B, ×416; C, ×600; D, ×120.

Shoot apices at older plastochron stages. Shoot apices at various advanced plastochron stages through to the 40th were examined. Surface photomicrographs of the area around the apical summit of the shoot apex at the 28th plastochron stage harvested 39 days after soaking showed that there was no group of cells surrounded by a thickened wall in the apical surface; it consisted of individual cells with walls of equal thickness (Fig. 9A). By comparing the surface photomicrographs with the paradermal sections (Fig. 9B), it was revealed that the cells #1~#5 were still single, while those #6~#9 had already divided into packets of two cells. These facts indicate that cell division occurs even in the summit of the shoot apices of old plants that have undergone a large number of plastochrons.

From the cellular configuration, the cells #1 and #2, the cells #3 and #4, and the cells #5 and #10 seemed respectively to be in groups, probably derived from the same initial of each, but this could be by no means substantiated, since there were no common thickened walls around each presumed group. The fact that visible cell
Figure 8. Shoot apex at the 17th plastochron stage 17 days after soaking. A, Montage photograph of the apical surface on the plus side of the meridians. White arrows in the flank indicate the points where the thickened walls encompassing cell groups disappeared. A vertical bar on the left indicates the axil of P1. B, Diagrammatic illustration of the vertical view of the same shoot apex. Shadowed area corresponds to the area of montage shown in A. Black arrow indicates the direction of the genetic spiral. A, ×360.

Figure 9. Shoot apex at the 28th plastochron stage 39 days after soaking. A, Surface photomicrograph taken from just above the apical summit. Arrow indicates the direction toward P1. B, Paradermal section cut nearly through the same area shown in A. ×600.

groups of more than three cells were not observed in the old shoot apex, where repeated cell divisions might occur, indicates that the cell progenies are not discernible beyond a few cells in such an adult shoot apex.

Discussion
Development of the cell group The occurrence of cell groups surrounded by distinctively dark-stained walls in the apical meristem of the shoot was pointed out
first by Ball (1949) for *Lupinus albus*. Since then, it has been depicted in a wide
variety of vascular plants by many investigators (Gifford, 1950; Boke, 1951; Mia, 1960;
Johnson and Tolbert, 1960; Gavaudan and Gastelier, 1970). Bierhorst (1977),
Hagemann and Schults (1978) and Imaichi (1986) showed cell groups surrounded by
common walls in the surface photomicrographs of the shoot apices of some ferns.

In the present investigation, the views of the superficial layer of the shoot apex of
*Lupinus albus*, by surface photomicrography of fresh material and by paradermal
sections, have demonstrated the development of cell groups during germination and
subsequent growth. The cell groups apparently begin by the anticlinal division of
individual cells in the surface layer of the shoot apex of an embryo within a few days of
imbibing water, though the divisions are not synchronous. As the derivatives divide
further and their number increases, the original cell wall stretches and becomes
thickened as shown by a dark staining appearance in paradermal sections. From
surface photomicrographs, however, the thickening of the original wall and even the
walls separating derivatives cannot be recognized until three or more derivative cells
are accumulated. As a plant gets older and successive foliar primordia are formed, the
number of derivatives within each cell group increases and the area of each cell group
becomes correspondingly larger, while the number of cell groups in the apical surface
decreases. The thickness of the surrounding wall becomes less conspicuous as the area
of the cell group increases, and finally there is no difference in thickness between the
surrounding wall and those of the derivatives, as examined by both surface
photomicrography and paradermal sections. This “equalization” is probably due to
the surrounding wall being stretched to a thickness equal to that of the derivative cells.

The development of cell groups described above indicates that every cell group
derives from its original single cell, the “initial cell”, as a result of its division and those
of its derivatives. The initial cell means here merely a mother cell of the cell group.
Therefore, it may be noted that any protodermal cell of the embryonic shoot apex
functions equally as an initial cell to form an individual cell group or “growth center”
(Ball, 1972) in the limited sense that it divides and contributes to the increased area of
the shoot apex. The cell groups derived directly from the initial cells in the surface of
the embryonic shoot apex and surrounded by the original thickened walls are referred
to tentatively as “primary cell groups”. Theoretically, daughter cells resulting from
the division of an initial cell might be expected to form secondary and further minor
cell groups as they divide further. In the illustrations of Bierhorst (1977), such
secondary, tertiary and further minor cell groups are clearly discernible within
segments of the apical cell in shoot apices of some ferns. In the present observations,
the secondary and tertiary cell groups are recognized within each primary cell group,
but further minor cell groups are not discernible, since any difference in thickness of
the walls of derivatives has not been recognized (Fig. 6). In older shoot apices the
groups of two or three cells are ascertained in the superficial layer of the summit area,
though their surrounding walls do not undergo thickening (Fig. 9). Apparently such
cell groups are not primary, but they indicate that cell division occurs anywhere in the
surface layer of the shoot apex.

**Cell division in the summit area** Cell divisions in the “central zone” of the shoot
apex, including tunica and inner corpus, have been reported by studies of paraffin
sections of fixed materials of various plants, either by counting the mitotic figures with or without pretreatment of colchicine or by labeling DNA (Gifford and Corson, 1971). Furthermore, by using time-lapse surface photomicrography, cell divisions were demonstrated in the same region for cultured living shoot apices of *Lupinus albus*, *Vicia faba* and *Asparagus officinalis* (Ball, 1960, 1962; Ball and Soma, 1965). Nougarède (1967) suggested that cell division might be induced by growth substances added in the culture media. Davis *et al.* (1979) discussed the traumatic effect of dissection of the shoot apex prior to labeling experiments upon mitotic activity in the central zone.

The present observations on the development of primary cell groups in the summit area of young shoot apices together with the existence of cell groups formed secondarily in the same area of adult shoot apices have provided further evidence for the division of cells located in the summit. Moreover, there are neither regular patterns in cell shape and arrangement nor regular segmentation pattern in cells located in the apical summit of the shoot apices of either young or adult plants of the present species, as far as the outer tunica layer is concerned. These facts may suggest that no stable group of a few cells (initials) is present there, as discussed by Bartels (1961) and Rogers and Bonnett (1989), and that the shoot apex should be regarded as a dynamic system of growth with continued positional change of cell population, as previously stated by Soma and Ball (1963) and Ball (1972).

**Analytical consideration of surface growth** On the basis of the fact that all of the primary cell groups on the apical surface have been derived from the initial cells constituting the protodermal layer of the shoot apex of the embryo, the following interpretation may be presented. By comparing the numbers of constituent cells or the surface areas of the primary cell groups in various portions of the apical surface, it is possible to compare the surface growth between the summit area and the flank. In the present study, it has been ascertained that the number of constituent cells of the primary cell group in the summit area is always smaller than that in the flanks, and that the lower a cell group is located on the flank, the larger becomes the number of its constituent cells (Fig. 6, Table 1). In older apices, while cell groups are still present in the summit area, no such cell group surrounded by thickened walls is discernible on the flank in surface photomicrographs (Fig. 8). These facts indicate a faster surface growth in the flank than in the summit area. In other words, more cell divisions have occurred in the flank than in the summit area and also more cell divisions in the middle flank than in the upper flank during the same period of time after soaking, provided that periclinal cell division rarely occurs in the outer tunica layer.

In considering the shoot apex at the 10th plastochron stage, while no group of cells appears on the flank along 0° M, the area above the axil of P1, many groups of cells are observed on the flank along 135° M in the surface photomicrograph (Fig. 6). However, while there are still several cell groups on the flank above the axil of P1, no such primary cell group is found on the lower flank between 135° M and 180° M of the older apex at the 17th plastochron (Fig. 8). Thus, there is a difference in the amount of surface growth between the flank along 0° M where the latest foliar primordium has been formed and the flank along 135° M where the next foliar primordium is about to arise. The latter is the site where the most vigorous surface growth has occurred on the
entire circumference of the apical dome, providing sufficient space for the initiation and development of the next foliar primordium. In addition, this flank portion consists of radially-arranged files of cells (Fig. 8) or radially-elongated cell groups (Fig. 6). These facts may suggest that the surface growth here has been mainly radial. However, it may be considered that these files of cells will be used up for the initiation of the foliar primordium at this site (I1) of the apical flank, and the vigorous surface growth will be shifted to another site (I2) for the following leaf to arise.

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